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Elevated CO_2 improves lodging resistance of rice by changing physicochemical properties of the basal internodes

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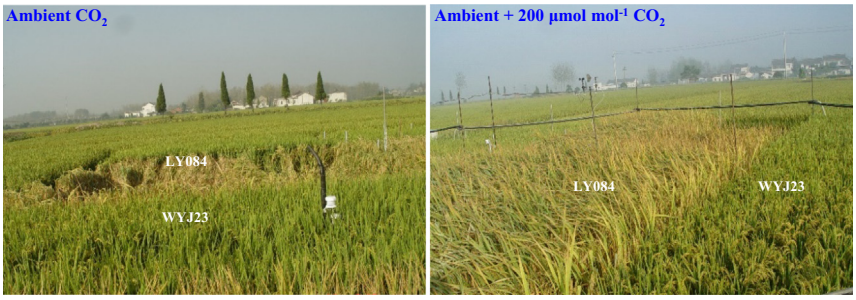
HIGHLIGHTS

- Lodging resistance of rice cultivars was investigated under fully open-air field.
- Elevated CO_2 decreased lodging incidence of the lodging-susceptible cultivar.
- Increases in culm density and starch content led to stronger breaking-resistance.
- Improved lodging resistance contributed to the yield gain from elevated CO_2.

GRAPHICAL ABSTRACT



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ABSTRACT

Elevated atmospheric CO_2 concentration has been shown to increase rice yield but its effect on plant lodging resistance is still under debate. In this study, we examined lodging incidence in the field and lodging-related traits of two rice cultivars with contrasting lodging susceptibility under ambient and elevated CO_2 (ca. 200 μmol mol^{-1} above ambient) concentrations by using a free-air CO_2 enrichment (FACE) system. Elevated CO_2 (E-CO_2) increased lodging resistance as shown by reduced visual lodging incidence in the field at the late grain filling stage in E-CO_2 plots. This coincided with enhanced in situ pushing resistance of intact plants one week before lodging occurred. The positive CO_2 effect was more pronounced in the lodging-susceptible cultivar LY084. In contrast, the cultivar WYJ23 displayed greater pushing resistance in the field, and no lodging occurred at either ambient or elevated CO_2 conditions throughout the cropping season. The field observations were consistent with the physicochemical characterization of basal internodes of rice plants at the grain filling stage. Greater lodging-resistance of WYJ23 was mainly attributed to its shorter plant height and thicker culm wall of basal internodes. The improvement of lodging resistance by E-CO_2 for the lodging-susceptible cultivar LY084 was mainly related to enhanced culm density, which was explained by elevated starch deposition in the stem. Less lodging incidence under elevated CO_2 contributed to an increase in grain yield by 36% for LY084. In conclusion, rice production could benefit from elevated CO_2 in a changing climate because of an increase in lodging resistance as a result of CO_2-induced improvements in mechanical strength of basal internodes.

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1. Introduction

Lodging is one of the major constraints for achieving high yield of small grain cereals including rice (Setter et al., 1997). Lodging in rice

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can be classified into stem lodging and root lodging, the former (also referred to as bending or buckling of the basal internodes) being the predominant form in transplanted rice (Islam et al., 2007). Lodging-induced self-shading reduces light interception of the plant canopy and thereby decreases photosynthesis, disturbs assimilation, water and nutrient transport into grains, and results in lower yields (Setter et al., 1997; Kashiwagi et al., 2010; Wu et al., 2012). In addition, lodged plant populations are exposed to high humidity and are therefore susceptible to diseases and pests, resulting in poor grain quality (Wu et al., 2012; Salassi et al., 2013). Also, lodging reduces mechanical harvesting efficiency and thereby reduces rice growers' profits (Kono, 1995; Salassi et al., 2013).

Lodging is difficult to control because it is a complex process determined by many factors including varieties, weather, soil type, crop management, and disease episodes. The introduction of semi-dwarf varieties in rice production substantially reduced lodging risk and increased the yield in the early 1960s (Chandler Jr, 1969). However, in recent years, the potential risk of rice lodging has been increasing because of the release of high-yielding varieties with large panicles, the increase of nitrogen fertilizer application, and shifts from labor-intensive transplanting to simplified planting techniques such as direct-seeding or seedling broadcasting (Duy et al., 2004; Lang et al., 2012; W.J. Zhang et al., 2014). In addition, extreme weather conditions such as typhoons accompanied by heavy rain at the late growth stage are other major reasons for lodging, which is predicted to occur more frequently due to global climate change (Ishimaru et al., 2008; Phelan, 2010). The occurrence of typhoons will increase by 2–11% in temperate regions at the end of this century because of global warming (Knutson et al., 2010; Masutomi et al., 2012). Since wind is the most significant dynamic factor that results in lodging (Berry et al., 2004; Gardiner et al., 2016), an increase in crop lodging will have increased negative impacts to crop production and food security.

The rise in atmospheric CO_2 concentration has been well recognized as the major global climate change factor (IPCC, 2013). Previous studies on rice responses to high CO_2 concentration were mainly focused on yield and grain quality, with less attention to lodging (Ainsworth, 2008; Yang and Peng, 2011; Wang et al., 2011). The majority of CO_2 fumigation experiments were conducted in closed or open-top gas chambers with limited space, which are not suitable for studying lodging, a phenomenon usually occurring under field conditions, with strong influence from the natural environment factors. Compared with chambers, the free-air CO_2 enrichment (FACE) system provides larger space for growing rice populations (Long et al., 2006). The plants grown in FACE are subjected to natural wind and rain, two environmental factors that favor lodging occurrence in the field.

Although FACE technology has been applied in rice since 1998 (Okada et al., 2001), only two reports about rice lodging in response to elevated CO_2 in FACE can be found, and the two experiments were conducted in Japan with relatively low N application (<15 g m^{-2}). Shimono et al. (2007) found that lodging risk of *japonica* rice increased with the increase of N application from 8 g m^{-2} to 15 g m^{-2}, but elevated CO_2 alleviated lodging risk at high N (15 g m^{-2}). Contrary to this, Zhu et al. (2013) found that elevated CO_2 had no significant effect on lodging risk of the Japanese cultivar Koshihikari and even increased lodging risk of the Chinese hybrid Sanyou63. However, the mechanisms underlying lodging responses to CO_2 and the influence of management and environmental factors remains poorly understood. On the other hand, the effects of elevated CO_2 on rice yields are more conclusive in short-term experiments: elevated CO_2 increases rice yield in general due to increases in tiller number and grain filling capacity (Ainsworth, 2008; Wang et al., 2015). Theoretically, a higher number of tillers per unit land area increases population density, and heavier panicles impose more pressure on culms. Both factors would increase lodging risk (Duy et al., 2004; Wu et al., 2012; Hirano et al., 2017). On the other hand, elevated CO_2 alters assimilate distribution within plant organs with a higher proportion of non-structural carbohydrates being stored in culms (Yang et al., 2006), which may increase the culm strength and reduce lodging susceptibility (Kashiwagi and Ishimaru, 2004; Ishimaru et al., 2008; Kashiwagi et al., 2006, 2008, 2010). Lodging resistance also depends on cell wall composition. Higher proportions of structural carbohydrates (lignin or/and cellulose) enhanced stem stability in rice (J. Zhang et al., 2014) and wheat (Nguyen et al., 2016), but some studies reported no clear relationship between lodging resistance and cellulose or/and lignin levels (Ishimaru et al., 2008; Kashiwagi et al., 2008; Frei, 2013; Gomez et al., 2018).

Two rice producing countries, Japan and China, have very different nitrogen fertilizer strategies in rice cultivation. The amount of N fertilizer applied per unit land area in Japan is relatively low with a maximum of 15 g m^{-2} (Shimono et al., 2007). In China, 25 g m^{-2} is the standard N level practiced by farmers, with some areas even reaching 35 g m^{-2} (Yang et al., 2006; Liu et al., 2008). Biomass responses to elevated CO_2 were greater when N supply levels were high (Ainsworth, 2008; Reich and Hobbie, 2013; Wang et al., 2015; Reich et al., 2018). However, high N application increased lodging risk in rice (Wu et al., 2012; W.J. Zhang et al., 2014). Therefore, it is important to understand how elevated CO_2 affects lodging in rice production area characterized by high N input. Hence, we conducted a FACE experiment in a rice field with two Chinese rice cultivars, WYJ23 (conventional *japonica*) and LY084 (hybrid *indica*) grown at ambient or elevated CO_2 (200 μmol mol^{-1} above ambient). The field lodging status was recorded and its association with lodging risk of whole plants and basal internodes was investigated. In addition, different lodging-related physico-chemical traits of the basal internodes were determined during the grain filling stage. The hypotheses are: (1) Elevated CO_2 changes stem properties and panicle size. These alterations induce changes in the overall mechanical properties of plants, and consequently affect lodging resistance of rice. (2) The CO_2-induced alteration in lodging resistance of rice contributes to its yield gain from elevated CO_2.

2. Materials and methods

2.1. Experimental site and treatments

Two rice cultivars representing two different rice types, the hybrid *indica* LY084 and the inbred *japonica* WYJ23, were grown in a paddy field located at the town of Xiaoji, Yangzhou, Jiangsu Province, China (119°42′E, 32°35′N), where a free-air CO_2 enrichment (FACE) experimental system was established. A full description of this set-up is provided by Liu et al. (2002). In brief, the FACE system consists of six octagonal plots having either elevated CO_2 levels (hereafter called E-CO_2 plots) or ambient CO_2 concentrations (hereafter called A-CO_2 plots). Each plot had a size of ca. 80 m^2. To minimize CO_2 contamination, each plot was at least 90 m away from the nearest other plot. In the E-CO_2 plot, pure CO_2 was emitted from the periphery towards the center through emission tubes located about 50–60 cm above the plant canopy. The rice canopy CO_2 concentrations were monitored and controlled by a real-time computer network. The CO_2 concentration in each E-CO_2 plot was constantly controlled at a level of 200 μmol mol^{-1} above the ambient plots through coordination by a CO_2 monitor, a wind sensor, a humidity sensor and a computer feedback unit that controlled CO_2 release. In the A-CO_2 plots, plants were grown under ambient CO_2 conditions without ring structures. The CO_2 fumigation began after seedling transplanting and continued until plant maturity. The treatment time in each day was from sunrise to sunset. The actual average daytime increase of CO_2 concentration during the fumigation period was 198.0 μmol mol^{-1}. Detailed descriptions of the soil properties for the site can be found in the previous publication (Jing et al., 2016).

2.2. Crop cultivation

Rice seeds were sown into a nursing bed on 20 May 2013, and then grown under ambient air for 30 days. Uniform seedlings were manually

selected and transplanted into subplots, which were distributed randomly in each plot of A-CO_2 and E-CO_2. Planting density was 1 plant per hill for LY084 and 2 plants per hill for WYJ23, because LY084 had greater tillering ability than WYJ23. This management ensured a similar population density during middle and late growth stages. Spacing of hills was 16.7 by 25 cm, equivalent to 24 hills m^{-2}. Nitrogen was applied as urea (N = 46%) and compound chemical fertilizer (N:P_2O_5:K_2O = 15:15:15%) at a rate of 22.5 g N m^{-2}. Forty percent of the total N was applied as basal dressing on 21 June, 30% was top-dressed on 28 June, and 30% was top-dressed on 25 July. Both P and K were applied as compound chemical fertilizer at a rate of 9 g m^{-2}. The water management was as follows: the paddy fields were submerged with water at a level of 5 cm from 20 June to 10 July. Then the paddy fields were subjected to wet-dry cycles through natural drainage and intermittent irrigation from 11 to 25 July, and the paddy fields were submerged with water again (about 5 cm in depth) from 26 July to 28 August. From 29 August to ten days before harvest the fields were subjected to wet-dry cycles again, and after that irrigation was terminated to allow paddy fields to dry for final harvesting. Diseases and insects were intensively monitored and controlled during the experiment period.

2.3. Sampling and measurements

2.3.1. Lodging incidence in rice field

Lodging incidence was determined as a percentage ratio of plants that lodged, excluding border plants, on 25 September, 1 October and 11 October. On each evaluation day, lodging incidence was measured in 680 hills per plot for A-CO_2 and 820 hills per plot for E-CO_2. Because no lodging or very little lodging occurred in FACE plots, the whole area of FACE plots for LY084, equals to 820 hills were surveyed. But for ambient plots, more than half of plants were lodged on the first survey. In order to make measurements more manageable, a relatively smaller patch equivalent to 680 hills with continuous plants were surveyed. The degree of lodging was classified into two groups based on the bending angles of the stems from the ground: <45° and ≥45°. The smaller angel indicated more severe lodging, because the plants with a smaller angle did not recover and were difficult to harvest mechanically. This simplified classification of stem lodging with a threshold of 45° was also in accordance with the measurements of pushing resistance of intact plants.

2.3.2. Pushing resistance of intact plants in the field

Pushing resistances of the whole plant was measured at 25 days after heading (DAH) for each cultivar, with a prostrate tester (YYD-1A, Hangzhou, China) according to the manual and the method reported by Kashiwagi and Ishimaru (2004). In brief, the prostrate tester was set in perpendicular direction to the plants at a height of 20 cm above the soil surface, and the pushing resistance (Newton, N) was recorded when the plants inclined at an angle of 45° to the vertical. Five representative plants in each plot were measured, the tiller numbers were counted, and the average value of the five plants represented the pushing resistance of the plot. The pushing resistances of single culms were calculated by dividing pushing resistance of the whole plant by the tiller number.

2.3.3. Culm morphology

After in situ measurement of pushing resistance, another six plants from each plot were taken from the field with the crown roots attached. After gently washing with water, the plants were separated into individual culms. Eight representative culms were selected and blotted dry with tissue paper. Stems were separated into individual internodes and numbered as 1 to 5, starting from the neck of the panicle and moving towards the base of the shoot. The length and fresh weight of each internode and panicle were measured. Since stem lodging usually occurs at the lower internodes (Seko, 1962; Hoshikawa and Wang, 1990; Islam et al., 2007; Gomez et al., 2017), only the physicochemical properties of the 4th internodes were measured after removing the leaf sheath. The breaking resistance of the 4th internode was measured according to Hirano et al. (2017) by using a prostrate tester (YYD-1A, Hangzhou, China). The distance between fulcra of the tester was set at 3 cm. The center of the internode was aligned horizontally with the middle point between the two fulcra, and the breaking resistance was measured at the center of the internode. The culm-wall thickness and the largest and smallest diameters of the basal internodes were measured by a caliper. After the measurement of fresh samples, the internodes were collected and dried at 80 °C for 72 h. The dry weights of internodes were determined.

The cross-sectional area, culm density, bending moment, and lodging index of each basal internode were calculated as follows:

Cross section area of 4th internode = longest × shortest diameters of 4th internode × π/4;

Dry weight per unit length of 4th internode = dry weight / length of 4th internode;

Bending moment of 4th internode = length × fresh weight of the plant from the lower node of 4th internode up to the panicle top × 0.001 × 9.8;

Lodging index of 4th internode = Bending moment of 4th internode / breaking resistance of 4th internode × 100. A high value of bending moment or lodging index indicates high lodging risk of a rice plant.

2.3.4. Chemical analysis

Dried internodes were ground into powder by using a Vibration Disc Mill (TS1000, Siebtechnik GmbH, Muehlheim an der Ruhr, Germany). The 0.5 g powder was digested in 5 ml concentrated H_2SO_4 with a few drops of H_2O_2 for 8 h at 250 °C. The digestion was diluted with deionized H_2O to 50 ml. The 50 ml sample was filtrated through quantitative filtrate paper, and the concentrations of K and P in the solution were determined by inductively coupled plasma spectrometry (iCAP 6300, Thermo Fisher Scientific, Franklin, USA). The filtrate paper together with the residue were transferred into a pre-weighted crucible and carbonized in an electric furnace. After carbonization, the sample in the crucible was incinerated in a muffle furnace at 920 °C for 30 min. After cooling down, the crucible was weighed again. The weight difference of crucibles corresponded to the weight of SiO_2 and Si concentration was calculated accordingly (Yang et al., 2004).

The starch concentration was determined according to Yang et al. (2001). In brief, the sample was extracted in 80% ethanol at 80 °C for 30 min, and the supernatant was discarded after centrifugation. The procedure was repeated three times. The residue was dried in an oven and extracted with 4.68 M perchloric acid for three times. The supernatants were combined and the starch concentration was analyzed by the method of Pucher et al. (1948).

Lignin concentration was determined spectrophotometrically according to Suzuki et al. (2009) based on the thioglycolic acid method. The pulverized samples were dried at 60 °C and extracted with water and methanol to obtain cell wall fractions. Then the samples were digested with thioglycolic acid to obtain the thioglycolic acid-lignin (TGAL) complex. Finally, the TGAL was dissolved in 1 M NaOH and the concentration was determined based on a standard curve using standard lignin (Sigma, St Louis, USA) dissolved into 1 M NaOH. The final lignin concentration was calculated based on total dry weight of internodes or the dry weight of cell wall material of the internodes.

2.3.5. Grain yield

Grain yield was determined at maturation in six hills of plants randomly selected from each plot. The grains were removed from panicles manually and then soaked in tap water (specific gravity = 1.0) to separate sunken and floated grains. Dry weight of filled (sunken) grains was determined after oven-drying at 80 °C for 72 h.

2.4. Data analysis

A split plot design was employed in the experiment with CO_2 levels as main plots and cultivars as sub-plots. Datasets were based on the mean values for each subplot when more than one individual measurement was taken. The analysis of variance (ANOVA) was performed using the statistical software Statistical Product and Service Solutions (SPSS 18.0, SPSS Inc., Chicago, USA) to detect the main effects of CO_2, cultivar and the effects of their interaction.

3. Results

3.1. Lodging incidence in rice field

The occurrence of lodging in modern rice production system is usually facilitated by external forces such as typhoons or heavy rain. In this study, the rainy and windy weather at the later grain filling stage was the trigger for lodging, which was observed immediately after the first extreme weather condition during 23–24 September, 2013 (Supplementary Table 1). The unfavorable weather continued and contributed to the acceleration of lodging towards harvest (Supplementary Table 1).

Significant genotypic differences between two rice cultivars in lodging incidence were observed (Fig. 1). Throughout the season, no lodging was observed in the resistant cultivar WYJ23 at either ambient or elevated CO_2 concentrations (FACE). For LY084, lodging first occurred in ambient plots at 32 days after heading (DAH), and the severity of lodging increased towards harvest, which was shown by both lodging incidence and the bending angle of stems (Fig. 1 and Supplementary Table 2). Averaged across three ambient plots, lodging incidence of LY084 was 51%, 62% and 100% at 32, 38 DAH and maturity, respectively. However, in FACE plots, lodging occurred only at plant maturity, with only 12% of lodged plants (Supplementary Table 2).

3.2. Pushing resistance of intact plant in rice field

Lodging-related traits of rice plants were measured at 25 DAH, when no lodging occurred in the field. The pushing resistance per hill of WYJ23 was significantly higher than in LY084 (Fig. 2). Elevated CO_2 significantly increased pushing resistance per hill of WYJ23 and LY084 by 30.6% and 39.3%, respectively. When taking the number of tillers per hill into account, the pushing resistance per tiller showed similar response to elevated CO_2 as pushing resistance per hill, but with a smaller increment (21.0% for WYJ23 and 28.8% for LY084), because elevated CO_2 increased the tiller number per hill of WYJ23 by 7.7% and LY084 by 7.0%, respectively.

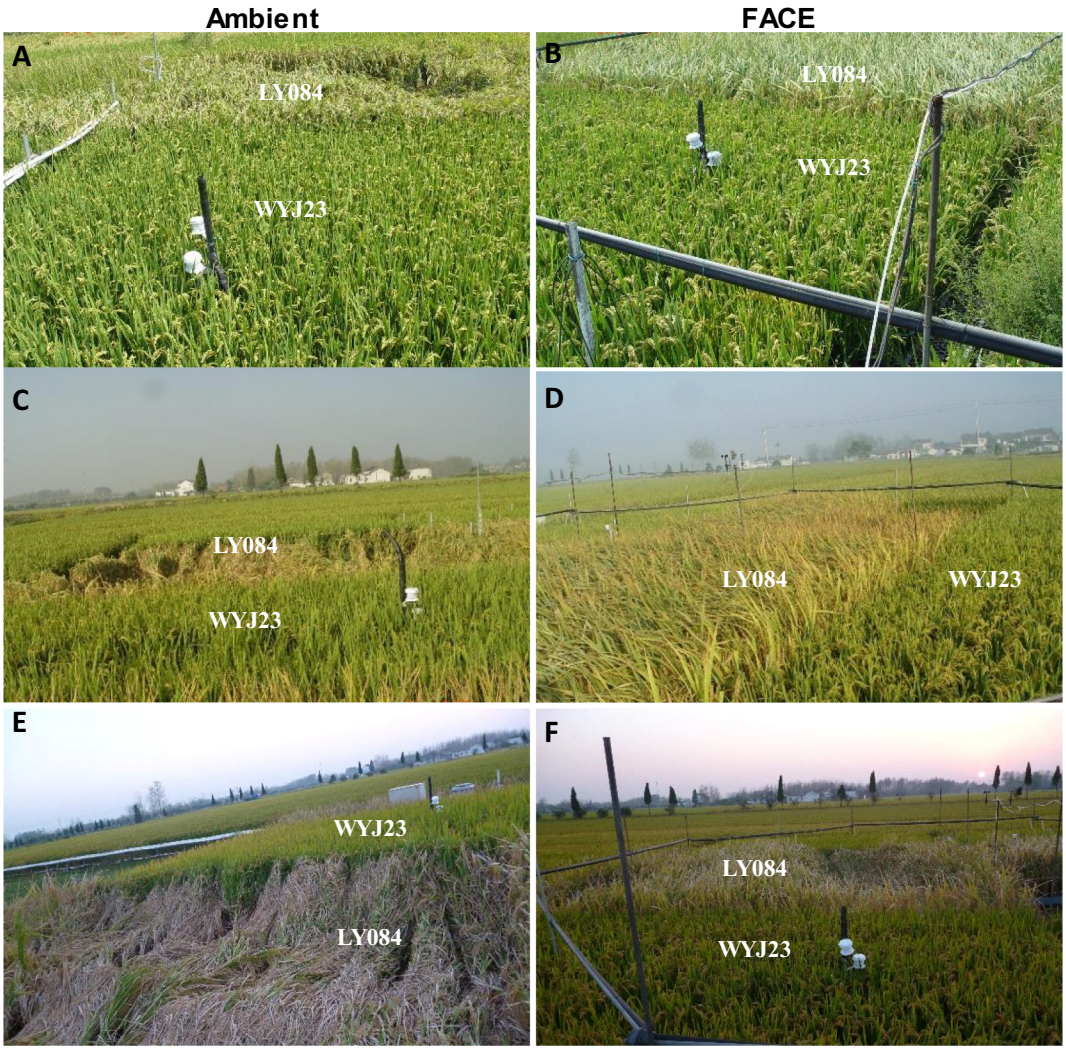

Fig. 1. Lodging incidence of two rice cultivars of WYJ23 and LY084 in field as affected by elevated CO_2 concentration. The representative pictures are shown for ambient and elevated CO_2 (FACE) plots at three-time points during grain filling stage of rice. A–B, Photographs took on 2013.9.25 (26 DAH for WYJ23, 32 DAH for LY084); C–D, Photographs took on 2013.10.1 (32 DAH for WYJ23, 38 DAH for LY084); E–F, Photographs took on 2013.10.11 (42 DAH for WYJ23, at maturity for LY084). DAH, days after heading.

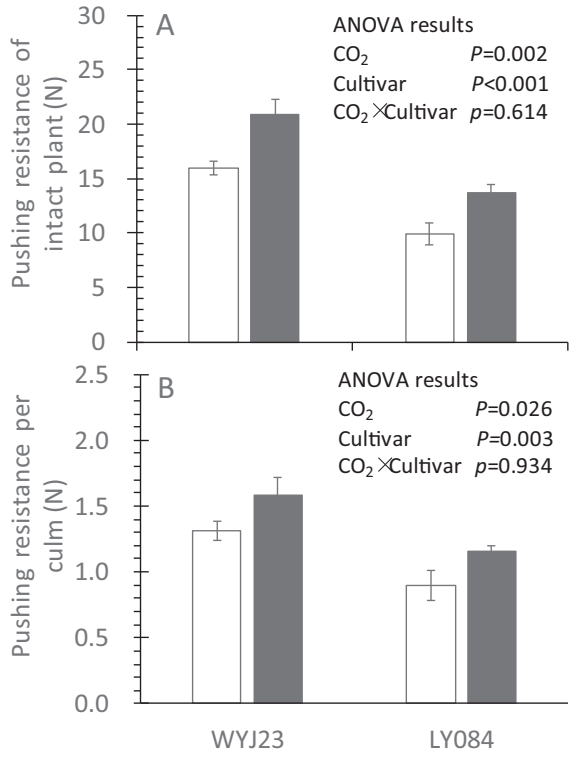

Fig. 2. The pushing resistance of intact plant (A) or culm (B) in the rice field measured at 25 days after heading. The two rice cultivars of WYJ23 and LY084 were grown at ambient (unfilled square) or elevated CO_2 concentrations (filled square) from transplanting until maturity. Values are means ± SE, n = 3. Each replicate is the average of values from five plants.

3.3. Lodging index of basal internodes

In agreement with the lodging incidence and pushing resistance of rice plants in the field, the lodging index of basal internodes also showed significant differences between the two cultivars (Fig. 3A). The lodging index of WYJ23 was less than half of that of LY084 at both ambient and elevated CO_2 concentrations. Elevated CO_2 decreased the lodging index of both rice cultivars to the same extend (11.0%). Lodging index is the function of bending moment and breaking resistance of the internode. The large difference between the two rice cultivars in lodging index was a consequence of both factors. The bending moment of WYJ23 was significantly lower (49%) than that of LY084 (Fig. 3B), while the breaking resistance of WYJ23 was significantly higher (28%) than that of LY084 (Fig. 3C). Elevated CO_2 increased the breaking resistance of basal internodes by 26.8% in LY084 and 10.4% in WYJ23, but no significant CO_2 by cultivar interaction was detected. In general, no significant CO_2 effect or CO_2 by cultivar interaction was detected on bending moment.

3.4. Characterization of bending moment

The bending moment of the basal internode was closely associated with plant height and weight. The culms and panicles of WYJ23 were significantly shorter than in LY084 under both CO_2 conditions. No significant CO_2 effect was detected for culm length as well as the length of each internode (Table 1). The dry weights of upper internodes were increased by elevated CO_2, especially for LY084 (Table 1). The CO_2-induced changes in the length and weight of internodes led to a significant CO_2 effect on the culm density, i.e. the dry weight per unit length of internode (Table 1). In general, the increase in culm density by E-CO_2 was greater in LY084 (11.9–28.1%) than in WYJ23 (4.6–18.0%), and

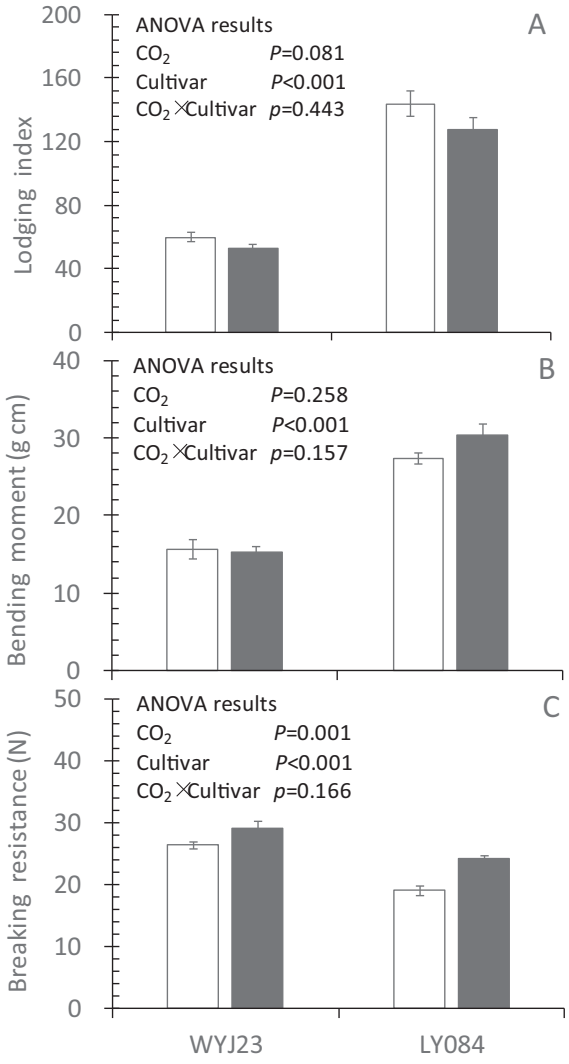

Fig. 3. The lodging index (A), bending moment (B) and breaking resistance (C) of the 4th internodes at 25 days after heading. The two rice cultivars of WYJ23 and LY084 were grown at ambient (unfilled square) or elevated CO_2 concentrations (filled square) from transplanting until maturity. Values are means ± SE, n = 3. Each replicate is the average of values from eight representative culms of six plants.

significant CO_2 by cultivar interactions were found for the 4th, 3rd and 2nd internodes.

3.5. Physicochemical characterization of basal internodes

The two rice cultivars differed in their morphology of basal internodes (Table 2). WYJ23 had significantly lower maximum internode diameter, minimum internode diameter and cross-sectional area than LY084, which indicated much thinner culms of WYJ23. However, the culm wall of WYJ23 was significantly thicker than in LY084. No CO_2 effect or CO_2 by cultivar interaction was detected in culm morphology traits of the basal internodes. Only Si concentration showed no significant response to elevated CO_2, while the concentrations of P and K were decreased by elevated CO_2 (Table 2). In addition, P concentration in LY084 was only half of that in WYJ23, but no cultivar differences were found for Si and K concentrations. WYJ23 had higher lignin concentration than LY084 irrespective of the calculation based on the total biomass or just the cell wall fraction of the internode (Table 2). CO_2 enrichment showed no effect on lignin concentration of the basal internode. In contrast, E-CO_2 increased starch concentration by 30.1%

Table 1
The internode length, weight and density of two rice cultivars of WYJ23 and LY084 grown at ambient or elevated CO_2 concentrations. The plants were sampled at 25 DAH for each cultivar.

Traits	WYJ23		LY084		ANOVA results		
	Ambient	FACE	Ambient	FACE	CO_2	Cultivar	CO_2 × cultivar
Internode length (cm)							
1st	29.5 ± 0.99	29.7 ± 0.42	40.8 ± 0.38	43.0 ± 0.63	0.112	<**0.001**	0.154
2nd	18.9 ± 0.66	18.3 ± 0.59	25.2 ± 0.87	25.7 ± 0.36	0.961	<**0.001**	0.425
3rd	13.1 ± 0.53	12.9 ± 0.18	16.8 ± 0.58	16.9 ± 1.07	0.933	<**0.001**	0.796
4th	8.3 ± 0.74	7.2 ± 0.44	7.7 ± 0.39	7.1 ± 0.61	0.171	0.593	0.672
5th	3.4 ± 0.32	2.6 ± 0.34	4.3 ± 0.18	4.3 ± 0.54	0.292	**0.007**	0.304
Panicle	17.2 ± 0.79	18.1 ± 0.44	26.2 ± 0.44	27.4 ± 0.14	**0.071**	<**0.001**	0.792
Dry weight of internode (g)							
1st	0.44 ± 0.03	0.45 ± 0.01	0.57 ± 0.01	0.68 ± 0.03	**0.024**	<**0.001**	**0.054**
2nd	0.42 ± 0.01	0.43 ± 0.02	0.57 ± 0.02	0.72 ± 0.01	**0.001**	<**0.001**	**0.002**
3rd	0.36 ± 0.01	0.40 ± 0.02	0.49 ± 0.02	0.60 ± 0.07	**0.089**	**0.002**	0.325
4th	0.26 ± 0.01	0.27 ± 0.02	0.26 ± 0.01	0.29 ± 0.03	0.239	0.785	0.705
5th	0.16 ± 0.01	0.15 ± 0.01	0.14 ± 0.01	0.17 ± 0.03	0.639	0.901	0.259
Dry weight per unit length of internode (mg cm^{-1})							
1st	14.4 ± 0.65	15.4 ± 0.17	14.0 ± 0.46	15.6 ± 0.30	**0.016**	0.774	0.475
2nd	21.4 ± 0.22	23.6 ± 0.21	22.3 ± 0.73	27.5 ± 0.91	<**0.001**	**0.004**	**0.034**
3rd	27.4 ± 0.47	30.2 ± 1.92	29.2 ± 0.46	37.1 ± 0.27	**0.001**	**0.003**	**0.038**
4th	34.1 ± 1.32	35.7 ± 0.97	33.1 ± 1.78	42.1 ± 0.71	**0.003**	**0.067**	**0.019**
5th	43.6 ± 0.94	51.5 ± 3.27	32.1 ± 1.86	41.2 ± 1.89	**0.004**	**0.001**	0.788

Significant effects at $p < 0.1$ are highlighted in bold. Values are means ± SE, n = 3. Each replicate is the average of values from eight representative culms of six plants.

in LY084 but only 3.9% in WYJ23, which led to a significant CO_2 by cultivar interaction at $p < 0.1$.

3.6. Correlation analysis

Correlations between lodging-related traits were investigated in LY084, which showed greater response to elevated CO_2. Lodging index was significantly positively correlated with internode length, but negatively correlated with breaking strength and starch concentration (Table 3). Dry weight per unit length of internode was positively correlated with pushing resistance of intact plants, pushing resistance per culm and breaking strength of the internode. Starch concentration was also positively correlated with pushing resistance of intact plants, pushing resistance per culm and breaking strength. Silicon concentration was negatively correlated with pushing resistance per culm, breaking resistance and starch concentration. Potassium concentration was negatively correlated with pushing resistance of intact plants, pushing resistance per culm and starch concentration. These results indicated that CO_2 enrichment improved the lodging resistance of LY084 through the increase in culm density, which was primarily caused by enhanced starch deposition in the stem.

3.7. Grain yield

The two rice cultivars showed no significant difference in grain yield at ambient CO_2, but at elevated CO_2 conditions, the grain yield of LY084 was higher than that of WYJ23 (Fig. 4). Elevated CO_2 increased grain yield of LY084 by 36%, but only 9% in WYJ23, resulting in a significant CO_2 by cultivar interaction.

4. Discussion

4.1. Genotypic differences in lodging resistance of rice

According to the lodging incidence in the field (Fig. 1), absence of lodging of WYJ23 but complete lodging of LY084 at grain maturity in the ambient plots confirmed that WYJ23 is a lodging-resistant and LY084 a lodging-susceptible cultivar. Based on the analysis of lodging-related traits of rice plants including culm morphology and physicochemical properties of basal internode, we found that the greater lodging-resistance of WYJ23 was attributed to higher breaking resistance and smaller bending moment of basal internodes (Fig. 3), and the latter was mainly due to shorter plant height (Table 1). Short plants can better resist lodging because of the lower gravity points, a principle

Table 2
Physicochemical characterization of the 4th internode of two rice cultivars of WYJ23 and LY084 grown at ambient or elevated CO_2 concentrations. The plants were sampled at 25 DAH for each cultivar.

Traits	WYJ23		LY084		ANOVA results		
	Ambient	FACE	Ambient	FACE	CO_2	Cultivar	CO_2 × cultivar
Morphological traits							
Maximum internode diameter (mm)	7.70 ± 0.28	7.33 ± 0.10	9.55 ± 0.28	9.73 ± 0.14	0.684	<**0.001**	0.249
Minimum internode diameter (mm)	6.67 ± 0.26	6.48 ± 0.17	8.52 ± 0.32	8.83 ± 0.04	0.789	<**0.001**	0.297
Cross sectional area (mm^2)	40.80 ± 3.06	37.60 ± 1.53	64.48 ± 4.42	67.64 ± 1.21	0.996	<**0.001**	0.298
Culm wall thickness (mm)	1.73 ± 0.07	1.63 ± 0.16	1.25 ± 0.09	1.12 ± 0.04	0.289	**0.001**	0.900
Biochemical traits							
Si (mg g^{-1})	23.21 ± 2.24	23.92 ± 1.46	22.46 ± 2.41	17.93 ± 1.32	0.348	0.117	0.210
P (mg g^{-1})	5.11 ± 0.24	4.50 ± 1.17	2.72 ± 0.12	2.29 ± 0.26	**0.036**	<**0.001**	0.663
K (mg g^{-1})	21.26 ± 2.66	14.55 ± 3.86	26.07 ± 3.86	15.18 ± 3.79	**0.040**	0.470	0.576
Lignin (% SDW)	4.97 ± 0.05	5.08 ± 0.19	4.07 ± 0.35	3.68 ± 0.11	0.529	**0.001**	0.262
Lignin (% CW)	5.99 ± 0.07	6.13 ± 0.14	5.02 ± 0.25	4.83 ± 0.15	0.886	<**0.001**	0.353
Starch (mg g^{-1})	104.4 ± 0.63	108.5 ± 7.01	66.1 ± 3.01	86.0 ± 1.51	**0.015**	<**0.001**	**0.077**

Significant effects at $p < 0.1$ are highlighted in bold. Values are means ± SE, n = 3. SDW, dry weight of internode; CW, dry weight of cell wall.

Table 3
Correlation matrix of lodging-related traits of LY084 exposed to ambient or elevated CO_2 concentrations.

	PRP	PRC	BR	LI	BM	IL	DWI	DWIL	MaxID	MinID	CSA	CWT	Si	P	K	Starch	LigninSDW	LigninCW
PRP	1																	
PRC	0.962**	1																
BR	0.808*	0.787*	1															
LI	−0.495	−0.584	−0.779*	1														
BM	0.736*	0.624	0.556	0.061	1													
IL	−0.395	−0.492	−0.529	0.891**	0.294	1												
DWI	0.528	0.418	0.290	0.321	0.939**	0.562	1											
DWIL	0.971**	0.939**	0.923**	−0.615	0.723	−0.439	0.487	1										
MaxID	0.676	0.738*	0.277	−0.259	0.265	−0.488	0.092	0.540	1									
MinID	0.746*	0.792*	0.434	−0.205	0.547	−0.298	0.354	0.663	0.903**	1								
CSA	0.706	0.764*	0.330	−0.208	0.404	−0.381	0.226	0.588	0.975**	0.974**	1							
CWT	−0.262	−0.225	−0.623	0.471	−0.319	0.050	−0.292	−0.427	0.481	0.339	0.449	1						
Si	−0.685	−0.811*	−0.826*	0.859*	−0.259	0.731*	0.009	−0.773*	−0.520	−0.605	−0.554	0.309	1					
P	−0.537	−0.398	−0.485	0.466	−0.149	0.481	−0.014	−0.513	−0.202	−0.001	−0.075	0.343	0.172	1				
K	−0.783*	−0.768*	−0.694	0.635	−0.300	0.742*	0.017	−0.767*	−0.776*	−0.746*	−0.758*	−0.090	0.717	0.524	1			
Starch	0.857*	0.813*	0.969**	−0.787*	0.515	−0.596	0.254	0.935**	0.352	0.417	0.358	−0.581	−0.767*	−0.676	−0.752*	1		
LigninSDW	−0.251	−0.029	−0.199	−0.150	−0.359	−0.048	−0.201	−0.235	−0.139	−0.234	−0.179	−0.190	−0.151	0.361	0.450	−0.237	1	
LigninCW	−0.238	−0.071	−0.070	−0.122	−0.170	0.133	0.006	−0.167	−0.403	−0.388	−0.400	−0.491	−0.099	0.328	0.577	−0.141	0.925**	1

PRP, pushing resistance of intact plant; PRC, pushing resistance per culm; BR, breaking resistance; LI, lodging index; BM, bending moment; IL, internode length; DWI, dry weight of internode; DWIL, dry weight per unit length of internode; MaxID, maximum internode diameter; MinID, minimum internode diameter; CSA, cross sectional area; CWT, culm wall thickness; Si, silicon concentration; P, phosphorus concentration; K, potassium concentration; Starch, starch concentration; LigninSDW, lignin concentration based on dry weight of internode; LigninCW, lignin concentration based on dry weight of well wall material. n = 6.

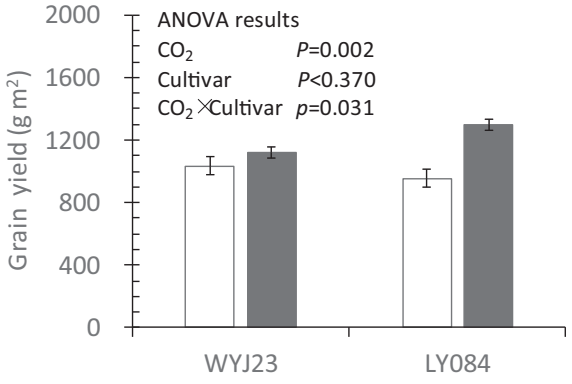

Fig. 4. Grain yield of two rice cultivars of WYJ23 and LY084 as affected by elevated CO_2 concentration. Values are means ± SE, n = 3.

that contributed to the lodging resistance of semi-dwarf rice carrying the Green Revolution *sd1* gene (Khush, 1999; Tomita, 2009; Hirano et al., 2017). The adoption of semi-dwarfing rice varieties has significantly increased grain, although further increases in yield potential are restricted by plant height (Peng et al., 2008). Recently, breeders tended to select varieties with increased plant height to further increase grain yield (G. Zhu et al., 2016).

Usually rice culms with higher breaking resistance were characterized by larger basal internode diameter or larger cross-section area of the culm (Ookawa and Ishihara, 1992; Kashiwagi et al., 2008; G. Zhu et al., 2016). However, in the present study, WYJ23 had thinner culms compared with LY084 as shown by lower internode diameter and cross-sectional area (Table 2). Thus, the greater breaking resistance of basal internodes in WYJ23 was mainly attributed to its thicker culm wall, in combination with other factors such as the higher concentrations of lignin and starch (Table 2). It has been well proven that more starch retained in stems during the grain filling stage can improve lodging resistance in plants (Kashiwagi and Ishimaru, 2004; Kashiwagi et al., 2006, 2010). The physical function of accumulated starch in the rigidity of stems is unclear, but starch content may affect turgor of stem cells (Ishimaru et al., 2008). Further investigation is warranted to understand the starch and how it affects mechanical traits. The role of lignin in lodging resistance of crops is still under debate (Frei, 2013). Higher lignin concentration is often associated with greater stem strength (Ookawa et al., 1993; J. Zhang et al., 2014; Weng et al., 2017), but on the other hand lignin makes cell walls more brittle compared to the more flexible cellulose (Frei, 2013).

The greater lodging resistance of WYJ23 was also reflected in the lodging index of basal internodes, which was less than half of that in LY084 (Fig. 3). Rice plants with small lodging indices are more tolerant to lodging than those with large lodging indices (Ookawa and Ishihara, 1992). At 25 DAH, the lodging index of WYJ23 was only 60. Even at plant maturity stage, the lodging index of WYJ23 was 100. In contrast, lodging index of LY084 already reached 140 at 25 DAH, which confirmed its lodging susceptibility.

4.2. Elevated CO_2 concentration increased the lodging resistance of rice plants

Lodging resistance was improved by elevated CO_2 in LY084 as displayed by lodging incidence in the field during the grain ripening stage (Fig. 1). The stronger lodging resistance under E-CO_2 was closely associated with changes in physicochemical properties of the basal internodes. The most significant change was the increase in culm density under E-CO_2 (Table 1), which was possibly caused by high amounts of starch retained in the stem. Other chemical components showed either no change or a trend of decrease upon elevated CO_2 (Table 2). This was confirmed by the significantly positive correlations between dry weight

per unit length of internode and lodging resistance parameters such as pushing resistance of intact plant (0.971**), pushing resistance per culm (0.939**) or breaking resistance (0.923**), as well as further positive correlations between starch concentration in the basal internodes and pushing resistance of intact plant (0.857*), pushing resistance per culm (0.813*) or breaking resistance (0.969**) (Table 3). These results are consistent with previous reports that elevated CO_2 increased non-structural carbohydrates proportions in stems (Yang et al., 2006), and that starch retained in stems during the grain filling stage can improve lodging resistance in plants (Kashiwagi and Ishimaru, 2004; Kashiwagi et al., 2006, 2008, 2010). A close relationship between lodging resistance and dry weight per unit length of basal internodes was previously found in 12 hybrids (Islam et al., 2007), and the authors further suggested that among all the morphological traits tested, the dry weight per unit length and breaking resistance of the lower internodes are primary targets for improving lodging resistance of hybrid rice in breeding program. Similarly, stem density was characterized as an important predictor of stem strength contributing to lodging resistance in sorghum (Gomez et al., 2018).

Except for starch, the concentrations of other lodging-related components (i.e., lignin, Si, K, P) measured in basal internodes of LY084 all showed a trend of decrease upon E-CO_2. This could be partially due to the "dilution effect" (Wang et al., 2011; McGrath and Lobell, 2013), implying that increasing the amount of a major component, i.e. non-structural carbohydrates by E-CO_2 dilutes the minor components such as mineral elements or lignin. Lignin has been associated with increased lodging resistance (Ma, 2009, 2010) or decreased lodging resistance (Frei, 2013), which makes its specific role in this study difficult to interpret. The concentrations of K and Si were often positively correlated with the breaking resistance of basal stems or lodging resistance in rice (Yang et al., 2004; Zhang et al., 2010). Although no direct measurements of cellulose in the present study, the study conducted on the same FACE site has showed that cellulose contributing to mechanical strength decreased by E-CO_2 (C.W. Zhu et al., 2016). Therefore, the contribution of the increase of starch to lodging resistance might outweigh the negative effects of the decreases in other compositions such as Si and K on lodging resistance of LY084.

In a previous study conducted in a Japanese rice-FACE site with relatively low standard nitrogen fertilization, the alleviation of lodging in cultivar Akitakomachi by E-CO_2 was associated with shortened and thickened lower internodes at an N application rate of 15 g m^{-2} (Shimono et al., 2007). In the current study, E-CO_2 decreased the lodging incidence independent of the internode length or thickness, since no significant changes in basal internode morphology by E-CO_2 were found (Tables 1 and 2). In addition to different cultivars used and climatic conditions, the controversial results can be attributed to differences in sampling dates and nitrogen levels in soil. In the previous studies, the measurements were conducted at grain maturity, but in the present study the samples were measured at 25 DAH before lodging occurred. Also the amount of nitrogen fertilizer used was higher in the China FACE site than that in the Japan FACE site. Despite the differences in the factors contributing to the increase in lodging resistance under high CO_2 conditions, both the study by Shimono et al. (2007) and present work concluded that E-CO_2 visibly reduced lodging in paddy fields, occurring due to heavy rains and strong winds. However, when no lodging occurred in the field, and the assessment was based only on lodging-related traits measured on detached plants, such an ameliorating effect could not always be confirmed (Zhu et al., 2013).

We demonstrated that E-CO_2 enhanced lodging resistance of rice by increasing the dry weight per unit length of internodes, which indicated that in future environments with high CO_2 concentration, the yield of hybrids may not necessarily be compromised by lodging because of the increased panicle weight: On the contrary, the yield potential of hybrids may be realized because of decreased lodging risk. In fact, the significant yield increase by 36% in elevated CO_2 in LY084 might partially be due to less lodging in E-CO_2 plots (Fig. 4), considering that the average yield increase of rice by E-CO_2 was only 20% according to a recent meta-analysis including FACE and non-FACE studies (Wang et al., 2015), and only 12% increase in FACE studies (Ainsworth, 2008). These results indicated that the CO_2-induced improvement in lodging resistance of hybrid rice contributed to its yield gain from elevated CO_2, especially under weather conditions favoring lodging.

In sum, the improvement of lodging resistance by E-CO_2 for lodging-susceptible cultivar LY084 was mainly related to enhanced culm density, which was explained by elevated starch deposition in the stem. The lodging related traits such as stem density may provide solutions for breeders to select for lodging resistant cultivars.

Declarations of interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.07.431.

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